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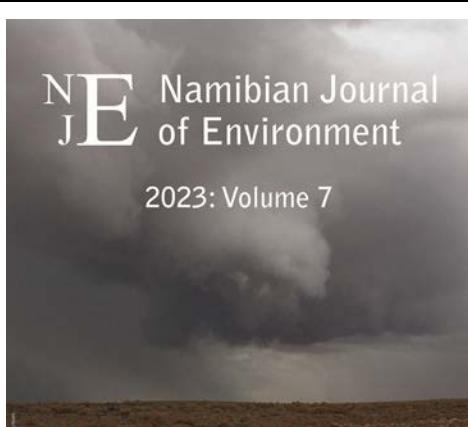
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The importance of large pans and surrounding bushveld for black rhino (*Diceros bicornis* ssp. *bicornis*) habitat use in the Kalahari: implications for reintroduction and range expansion

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ABSTRACT

In the Kalahari region of southern Africa, recurrent droughts can affect local livestock production and even lead to the loss of traditional farmland. As a result, the wildlife economy has grown in importance as a profitable approach to the sustainable use of native game species adapted to these challenging climatic conditions. This has led to restoration efforts in the region that have brought back wildlife including the critically endangered black rhino (*Diceros bicornis*). To understand the interrelationship between a reintroduced black rhino population and a rural Kalahari wildlife reserve, this research project aimed to decode the key drivers of black rhino habitat use based on a multiscalar approach of combined aerial and ground information on ecogeographical variables (vegetation and artificial habitat components) together with spatial rhino location and individual movement data. On average, black rhino home ranges were found to be $67 \pm 20 \text{ km}^2$, with core areas of $24 \pm 11 \text{ km}^2$. These are predominantly covered by the landscape types of bushveld and calcareous pans. Analysis of the different landscape factors present in the reserve showed that vegetation heterogeneity, vegetation density, vegetation damage, browse availability and waterhole density were significantly higher in the pooled core areas of the total population compared to less frequented areas. Furthermore, a binary logistic regression model predicted that browse availability and vegetation heterogeneity of medium to large woody species to be the most significant effect on black rhino habitat use. The model also showed a negative correlation with *Acacia* spp. saplings, which can be explained by the decline or absence of saplings in the core areas due to the continuous feeding pressure of black rhinos and other herbivores. Evaluation of black rhino habitat use and spatial distribution indicates a strong preference for the mosaic of microhabitats around calcareous pans and surrounding lunette dunes covered by bushveld. Together with the year-round availability of water (rain-fed lakes and artificial waterholes), these focal points are of high ecological importance and provide suitable habitat conditions that may highlight the potential for further black rhino reintroduction and range expansion, as well as general rewilling efforts in the region.

Keywords: biodiversity, browse, bushveld, carrying capacity, drought, ecogeographical variables, home range, Namibia, rewilling, rhino conservation, spatial distribution, vegetation, wildlife economy

INTRODUCTION

Over the past century, the translocation of wild animals has become an important tool for managing, restoring and enhancing declined populations (Langridge *et al.* 2020). Translocated animals must adapt to a new environment and quickly establish natural behavioural patterns, which are part of the acclimatisation process (Mazess 1975, Göttert *et al.* 2010). The conservation of the black rhinoceros (*Diceros bicornis*) is a good example of how translocations of individuals and small populations have helped expand the species into its former range and increase overall population numbers (Göttert *et al.* 2010).

With the establishment of rhino sanctuaries throughout the African continent, rhinos can be reintroduced into protected areas where they have

gone locally extinct in the past. For several decades, translocation has been a common practice, taking place from high-risk areas and government lands to private lands (Emslie & Brooks 1999). In comparison to large state-owned national parks, such sanctuaries can be found in established private wildlife reserves or game farms which are safeguarding other wild animals in a confined area. In some cases, the protective attributes of these sanctuaries outweigh their habitat suitability (Adcock *et al.* 1998, van der Heiden 2005). As an example of such range expansion projects, Namibia's Black Rhino Custodianship Programme (BRCP) is a rhino conservation success story built on nationwide rhino sanctuaries, spread across 10 communal conservancies and 25 freehold ranches. It also embodies several aspects of effective ecological population management in line with international guidelines (Kötting 2020, Muntifering *et al.* 2023).

Conservation of the black rhino in Namibia faces chronic challenges, i.e., despite an ongoing poaching crisis, some local populations continue to exceed the carrying capacity of conservation areas. Maintaining and expanding this conservation programme is expensive, and generating sufficient revenue is a challenge (Kötting 2020). While many privately owned areas in the central and northern regions of Namibia are already part of the programme, other areas are becoming increasingly important for potential reintroduction and range expansion. An example of this is the Kalahari region in central-eastern Namibia, which has received limited attention from the conservation programme to date, despite representing a large proportion of Namibia's land area (Kötting 2021). Precolonial historical records indicate that both species of rhino were once common in central-eastern Namibia (today's Omaheke region, part of the Kalahari ecosystem), making the Kalahari an important refuge for both rhino and many native wildlife species (van Rooyen *et al.* 2008, Wallgren *et al.* 2009, Sullivan *et al.* 2021).

A principal geomorphic feature of this semiarid landscape is depressions or pans, which vary in size and which are scattered throughout the entire region. The pans are important temporary water reservoirs during the rainy season and are characterised by relatively high mineral content and, in some cases, perennial grass cover (Lancaster 1974, Parris & Child 1973). Wind erosion deposits sediment from the pans into the surrounding area to form flanking lunette dunes (Haddon 2005). The pans and their surroundings contain a high diversity of vegetation and landscapes, are critical for wildlife species, and are particularly selected and used for keeping livestock from nearby settlements (van Rooyen & van Rooyen 1998, Parris & Child 1973). As many parts of the central and southern Kalahari have been converted to pastoralism, human activities such as overgrazing by livestock have had a negative impact on vegetation conditions around the pans, resulting in bush encroachment and reduced amounts of perennial grasses and plant litter (Parris & Child 1973, Moleele & Mainah 2003, Wallgren *et al.* 2009).

The Kalahari is affected by extreme weather events such as recurrent droughts, which threaten the livelihoods of local communities and lead to increased livestock mortality, crop failure and even loss of farmland (Mogotsi *et al.* 2013). Although droughts have occurred throughout history, ongoing climate change is accelerating and amplifying these events, leaving poorer households with limited resources to adequately cope and adapt (Mogotsi *et al.* 2011, 2013). A common consequence is an increase in internal displacement and migration (Adaawen *et al.* 2019).

The combination of such critical environmental, socioeconomic and climatic factors is encouraging a rethink of land use patterns in many regions of Africa, with an increased emphasis on the sustainable use of wildlife, which is more adaptable to challenging site factors than traditional livestock. The wildlife economy is a diverse sector that combines ecotourism, the sale of live animals, various forms of hunting and meat production (Child *et al.* 2012). This profitable approach has extended to the Kalahari, enabling rewilding efforts to restore ecological balance and promote biodiversity, particularly for threatened and keystone species such as the black rhino. As an example, Kuzikus Wildlife Reserve (KWR), a former cattle farm negatively affected by decades of livestock grazing, has been transformed into a wildlife sanctuary, with more than 40 years of ecological restoration. The reserve's main source of income is ecotourism, but it is also a representative site for the BRCP, providing suitable conditions for analysing habitat use in the Namibian Kalahari and investigating the ecosystem's value for black rhino reintroduction and range expansion. KWR was approved as one of the first reintroduction sites under the programme in the late 1990s and over the past 25 years the population has grown remarkably. Its high population growth rate of 9% lies above the Namibian BRCP average of 7.9% (net of translocation) and 8.5% (net of translocation and poaching), as well as the IUCN benchmark of 5% (Emslie *et al.* 2019, Sullivan *et al.* 2021, Reinhard & Reinhard 2022).

Several studies have addressed the issue of black rhino habitat use, resource selection, spatial distribution and habitat suitability assessment, testing different methods and models. One of the recent studies from 2015 used random forest models to predict habitat use (Lush *et al.* 2015), another from 2012 focused on logistic regression and Bayesian Information Criterion (Buk 2012), Simon Morgan (2010) included a maximum entropy (Maxent) model and van der Heiden (2005) worked with a utilisation distribution. As the first black rhino home range and habitat use study of its kind in this landscape and ecoregion of Namibia, it is important to understand the full picture of how specific ecogeographical variables (EGVs) of the Kalahari ecosystem, as well as species-habitat interactions, affect the spatial distribution of a reintroduced black rhino population. This, in turn, may help to maintain viable populations, improve local management strategies and even promote further conservation efforts in the Kalahari ecosystem (Göttert *et al.* 2010, Morgan 2010).

METHODS

Study site and landscape

The study took place in the Kuzikus Wildlife Reserve

which is located approximately 150 km southeast of the Namibian capital, Windhoek, at 23°16'–23°26'S and 18°33'–18°48'E. The private reserve covers around 115 km², lies about 1,350 m above sea level and is mostly flat, except for three dunes of about 15 m in height. It is surrounded by a perimeter fence, and the lodge and staff village have an additional interior fence. Ecotourism has been active in the reserve since 2005 and includes regular human activity, mostly focused on guest-related activities such as game drives, nature walks and horse riding, as well as management activities such as road, waterhole and fence maintenance, anti-poaching patrols, and occasional game management and ecosystem drone mapping operations.

KWR can be divided into six different vegetation types, comparable to those of the Kalahari Gemsbok National Park in South Africa (now part of the Kgalagadi Transfrontier Park) (van Rooyen *et al.* 2008, Sterk 2019). The area belongs to the southern Kalahari, part of the Acacia Tree-and-Shrub Savanna biome (Figure 1) (Atlas of Namibia Team 2022). The most common vegetation type, the low duneveld, occupies 46% of the reserve and is characterised by *Acacia erioloba* and *Schmidtia kalahariensis*. In contrast, the bushveld covers almost the other half of the landscape and is dominated by different *Acacia* spp., mainly *Acacia mellifera*. As the bushveld appears to vary locally, two parameters (bush density and dominant species present) were used to differentiate bushveld, resulting in three distinct

bushveld types (mixed bushveld, open *A. hebeclada* bushveld and dense *A. mellifera* bushveld). Depressions are found in 12 calcareous pans, two of which are large (1.9 and 0.8 km²). The sandy grassveld forms the landscape between the high dunes and contains a very low proportion of woody vegetation.

Previous study

The home range and habitat use analysis follows up on a previous study on the carrying capacity of black rhinos in the KWR from 2018 to 2019, and integrates its findings on how habitat and food resources limit population growth. For KWR, the Southern African Development Community's Rhino Management Group (SADC RMG) Black Rhino Carrying Capacity model v.2 predicts a total browse availability score of 7.95% and a mean ecological carrying capacity estimate of 11 black rhinos on the 115 km² property (Table 1) (Sterk 2019). Black rhino browse availability (BA) is defined as the landcover which describes the percentage of available food plants in a three-dimensional space between 0 and 2 m height (Adcock 2017).

Study population and other herbivores

During the period of data collection, ten individual black rhinos were present in the reserve; two territorial bulls, two subadult bulls and three adult cows, each accompanied by one calf. Each individual was given a name and all adult animals have specific ear notches to facilitate identification. The reserve

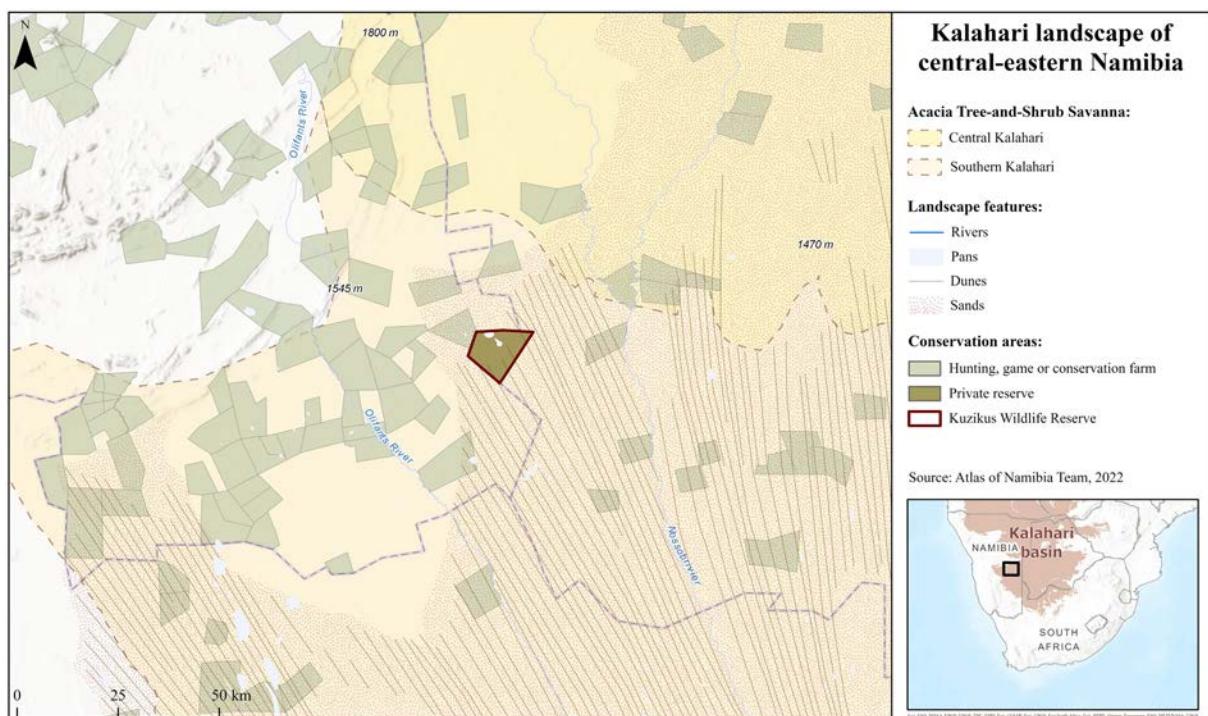


Figure 1: Map of the Kalahari landscape (Namibia) showing the location of Kuzikus Wildlife Reserve within the Kalahari, the extent of the Acacia Tree-and-Shrub Savanna, characteristic landscape features and conservation/wildlife areas (Atlas of Namibia Team 2022).

Table 1: Average black rhino browse availability values for each vegetation type found in Kuzikus Wildlife Reserve expressed as the percentage of land cover. Analyses were done using the black rhino carrying capacity model v2 (Sterk 2019).

	Low duneveld	Mixed bushveld	Dense bushveld	Open bushveld	Sandy grassveld	Pan
Average browse availability	5.7%	9.7%	12.4%	1.2%	0.2%	0.9%
Percentage of land area	46.0%	32.0%	17.5%	1.1%	0.5%	2.9%
Vegetation type contribution to total browse availability score	2.622%	3.117%	2.167%	0.013%	0.001%	0.027%
Total browse availability score for Kuzikus Wildlife Reserve: 7.95%						

also hosts several species of browsing herbivores that compete with black rhino, including Angolan giraffe (*Giraffa giraffa angolensis*), common eland (*Taurotragus oryx*), greater kudu (*Tragelaphus strepsiceros*), gemsbok (*Oryx gazella*), common impala (*Aepyceros melampus*), springbok (*Antidorcas marsupialis*), common duiker (*Sylvicapra grimmia*), and steenbok (*Raphicerus campestris*).

Data collection

Home range studies, as well as understanding habitat use, require a large number of location points from individual black rhinos for statistical analysis. This is typically achieved using VHF and GPS collars (horn implants or anklets) (Seidel *et al.* 2019). Darting and collaring rhinos is a costly operation involving helicopters, vets, ground staff, drugs, and technical equipment, and is also stressful for the rhinos (Morkel 1994). To avoid such events, a mix of sampling methods was used in this study. Georeferenced location data points were collected over a period of ten months (between June 2021 and April 2022). Data collection consisted of direct field observations, via identified footprints, evaluated night-vision camera trap images, operational drone flights for anti-poaching and ecosystem mapping, and external data points from other reserve staff.

The approach to visually locate individuals and map corresponding footprints was based on a stratified random survey method, with the reserve divided into four zones. Within each zone, vehicle and random off-road foot patrols were conducted to monitor rhino activity. Zones were then rotated on a daily basis, with the reserve's road network allowing rapid access to all areas. In open areas, rhinos could be spotted at distances of more than 1 km. Random foot patrols were also conducted frequently to access areas of dense vegetation with limited visibility, looking for rhino tracks and signs. Two night-vision camera traps were placed at waterholes, salt rocks, dung middens and rhino 'highways', rotating between these sites every 3–4 days, while an additional six camera traps were placed at random locations within the reserve and moved to a different site each week. To avoid

bias caused by frequent rhino activity around waterholes, information on their location was placed on identified trails that were at least 250 m away from the waterholes.

To link rhino footprints to individuals, each rhino was tracked at least once at the beginning of the study to obtain clear footprint images in bare substrate, resulting in a verified identification catalogue. Subsequently, when rhino tracks were found, footprint identification was based on visual comparison of heel line patterns, which are unique to each rhino. This non-invasive approach can be reliable with high accuracy in small populations (Jewell *et al.* 2020).

Sightings were added into the database if separated by at least one day, implying that information on each individual rhino could only be recorded once a day. Nearly all activities were conducted either in the early morning or late afternoon hours, as most of the rhinos were active at these times. All rhino related data include information on date, time, ID of the individual, its behaviour, whether there was a change in behaviour caused by the observation and the method used for data collection. To map rhino locations, GPS data points were logged on the ArcGIS Explorer App for IOS (Esri Inc. 2018–2020).

Habitat use was determined taking different EGVs into consideration. Based on literature review, the following variables were chosen for their important role in rhino habitat use and preference: 'browse availability' (related to the vegetation type); 'vegetation density'; 'vegetation heterogeneity'; 'vegetation damaged by rhinos'; 'Acacia spp. sapling distribution'; 'availability and distance of permanent water points'; 'intensity of road use' (van der Heiden 2005, Morgan 2010, Buk 2012, Lush *et al.* 2015).

In November 2021, as part of the Kuzikus Mapping Project (see <https://kuzikus-namibia.com/research>), a two-week drone mission using a SenseFly eBeeX fixed-wing aircraft, flown at an altitude of 160 m, collected 3 cm high-resolution RGB imagery to build an aerial imagery database of the entire reserve. The

mission was timed to capture medium to large vegetation at the end of the dry season and just before the first rains of the wet season, allowing optimal visualisation and accurate delineation of landscape and vegetation components. These high-resolution drone images, supplemented by publicly available satellite data and validated through a ground-truthing process, were used to map all distinctive landscape features, vegetation types, their densities and artificial elements (waterholes, fences, buildings and roads) within the reserve's infrastructure. These digitised features were then integrated into ArcGIS to create a geospatial 'digital twin' with defined boundaries of the different features (Esri Inc. 1999–2019).

During the same period, a vegetation survey of the reserve was carried out. For this purpose, a digital grid consisting of square grid cells measuring 750 m x 750 m was created over the study area using ArcGIS. A total of 260 cells were generated, and the midpoint of each cell was marked as the location for establishing vegetation plots (Esri Inc. 1999–2019). Consequently, the vegetation data obtained from each plot represented the corresponding grid cell. Along the reserve boundary, plots were positioned as centrally as possible.

The 50 m diameter vegetation plots were used to manually record key aspects of the vegetation, consisting of the vegetation heterogeneity (number of woody species), the extent of damage caused by black rhino browsing (expressed as a score) and the presence of *Acacia* spp. saplings (counted individuals). In addition, browse availability values derived from data from the previous carrying capacity study were assigned to the different vegetation types found in the reserve. These relative values were also integrated into the corresponding grid cells.

On completion of the plot survey, the response data for each vegetation variable was divided into four categories (absent/very low, low, medium and high) and assigned accordingly, resulting in a scorecard. This helped to better visualise the data in the next step (Table 2).

Table 2: Ecogeographical variables scorecard by category per 50 m diameter vegetation plot, including vegetation damage (score), vegetation density (number of trees and bushes), vegetation heterogeneity (number of woody plant species), *Acacia* spp. saplings (number of saplings), browse availability (score) grouped into four categories (absent/very low to high).

Category	Vegetation damage	Vegetation density	Vegetation heterogeneity	<i>Acacia</i> spp. saplings	Browse availability
	(score)	(Number of trees and bushes)	(Number of woody plant species)	(Number of saplings)	(score)
Absent/very low	0 – < 1	0	0 – 2	0	0 – < 3.25
Low	1 – < 3	< 20	3 – 4	1 – 3	3.25 – < 6.5
Medium	3 – < 5	20 – 40	5 – 6	4 – 6	6.5 – < 9.75
High	≥ 5	≥ 40	≥ 7	≥ 7	≥ 9.75

For the artificial habitat features, the availability, distances and densities of water points were assessed using the digital twin, while road transects were assigned to a specific category indicating the frequency of weekly use. Subsequently, these data were also integrated into the grid cell database.

Data analysis

Based on the rhino location points, individual home ranges were estimated and combined to a pooled population model using the Kernel Utilisation Distribution (KUD) estimation in R with the package 'adehabitatHR' (Calenge & Fortmann-Roe 2015).

When examining habitat use, the characteristics of the core ranges were particularly considered, which are salient areas that include 50% of all the nearest location points, demonstrating a direct preference for the area (Lent & Fike 2003).

Chi-squared and Fisher's tests were applied to assess significant differences between vegetation types within the core and peripheral areas of the rhino range. In addition, analysis of variance (ANOVA), T-tests and Tukey tests were used to determine significant differences in the distributions of vegetation heterogeneity, vegetation density, damaged vegetation, waterhole density, waterhole distance and road transect (use categories) between the core and peripheral areas (** p ≤ 0.001; ** p ≤ 0.01; * p ≤ 0.05).

To evaluate the interaction of EGVs and their impact on rhino habitat use, multicollinearity between the single variables was calculated using a variance inflation factor (VIF). A value of 1 indicates no correlation, a value between 1 and 3 indicates a moderate correlation and values > 3 represent strong correlations and can be excluded as coefficient estimates, while p values in the regression output are likely to be unreliable (R Core Team 2018, Statology 2021).

Secondly, a binary logistic regression model (BLRM) and the odds ratio of each variable was calculated using the grid cell database combined with the response variable 'core area' ('Yes' or 'No') (Harrell 2015).

The model was checked in advance for its meaningfulness. This included an omnibus test to find out whether the test model makes a significant explanatory contribution compared to the null model. A chi-squared probability was identified for this and checked if the R-squared value can be applied as a goodness-of-fit measure for logistic regression models using the Nagelkerke method (Nagelkerke 1991).

The odds ratio (OR) is a useful way of assessing the likelihood of an outcome occurring given a particular exposure. If the OR value is > 1 , an increased occurrence of the event can be expected. An OR value < 1 indicates a decreased occurrence of the event (Tenny & Hoffmann 2021). In terms of black rhino habitat use, this means that if the categorical value of each variable increases by one unit, the probability of an area being considered a rhino core area will either increase or decrease by the given OR value.

RESULTS*

**Maps showing rhino locations, home ranges, habitat use, or reserve infrastructure are withheld for security reasons.*

A total of 518 rhino location points were recorded during the study. Direct observations provided 296 data points, 167 were derived from footprints, tracks and signs associated with individual rhinos, 52 data points are from camera traps and three individuals were spotted during operational drone flights.

Due to the topography, the black rhino population has access to almost the entire available area within the perimeter fence, excluding the inner fenced reserve infrastructure. The pooled spatial distribution of all individuals covers 112 km^2 (95% isopleth) and core areas 60 km^2 (50% isopleth). The following spatial categories refer to the core and peripheral areas of the home ranges. Unused areas are almost non-existent and of no further significance.

The spatial distribution of the population is largely based on the two separate home ranges of the two dominant bulls, Columbus and Hermes. In contrast, the home ranges of females and subadult bulls show that they predominantly share the same areas, are similar in size and fully overlap with the core area of Columbus. On average, individual home ranges are $67 \pm 20 \text{ km}^2$ (95% isopleth) and core areas are $24 \pm 11 \text{ km}^2$ (50% isopleth) (Table 3).

Vegetation types vary significantly between the core and peripheral areas of the pooled total rhino population range (Fisher's test: $p < 0.0005^{***}$). The core areas are dominated by bushveld types, which occupy 70% of the area, while low duneveld occupies 25% and pans 5%. No sandy grassveld was recorded in the core areas. On the other hand, low duneveld is the most common vegetation type in the outer areas of the pooled home ranges, covering more than 70%. Mixed bushveld and dense bushveld cover comparatively less land at 19% and 9% respectively. Calcareous pans were not found to be used in the peripheral areas (Figure 2).

During the spring season in September and October, a shift in the range of female rhinos was observed. At this time, they mainly visited the dune system. During the remaining months of the study period, the females remained in the bushveld areas of the reserve. The 50% isopleth of their range was 18 km^2 in spring and 12 km^2 during the rest of the year. No seasonal shift in the distribution of bulls was observed.

Data analysis of the natural EGVs present in the wildlife reserve showed vegetation heterogeneity ($p < 0.0001^{***}$), vegetation density ($p = 0.0063^{**}$), vegetation damage ($p = 0.0004^{***}$) and browse availability ($p = 0.0005^{***}$) were significantly higher in the pooled core areas of the total population compared to the less frequented peripheral areas. No significant differences in the number of *Acacia* spp. saplings were found between the two types of areas ($p = 0.240$) (Figure 3).

Table 3: Home range size estimation (50% and 95% isopleths) for individual rhinos in the Kuzikus Wildlife Reserve (including information on sex and year of birth) and ratio of 50% isopleth size to 95% isopleth size. For females, calf names and year of birth are shown in brackets.

ID adults (and calves)	Sex	Year of birth	Sample contribution (n)	50% isopleth (core area) in km^2	95% isopleth (home range) in km^2	Ratio 50% to 95% isopleth
Columbus	male	1992	92	45	91	0.49
Hermes	male	2002	102	8.5	25	0.34
Hector	male	2016	68	25	71	0.35
Helia (Hades)	female (male)	2007 (2021)	71	22	64	0.34
Juno (Jonas, Jakari)	female (male, male)	2005 (2015, 2019)	110	18	67	0.27
Kenia (Kauri)	female (female)	2008 (2021)	75	23	69	0.33

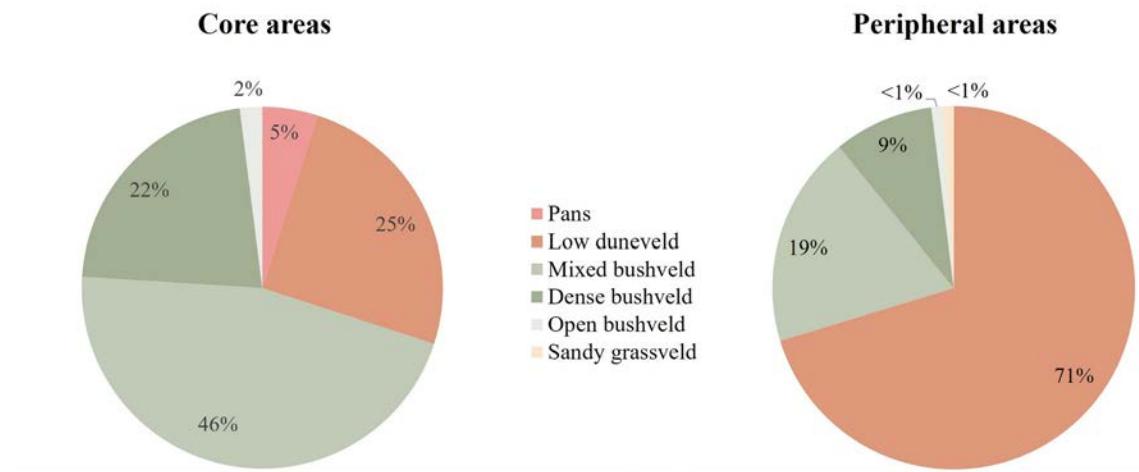


Figure 2: Distribution of vegetation types within black rhino core areas and peripheral areas in the Kuzikus Wildlife Reserve.

For the artificial habitat variables, we found that waterhole density is significantly higher in the core areas of the pooled rhino home ranges (1.8 waterholes per 10 km²) compared to the peripheral areas (0.6 waterholes per 10 km²) ($p = 0.0002^{***}$). However, there is no statistically significant difference between the two area types in terms of mean distance between nearby waterholes ($p = 0.091$) and the frequency of road use ($p = 0.065$) (Table 4).

Within the binary logistic regression, the variables were first tested for multicollinearity. No values were excluded from further interpretation as none exceeded a value of 3. The highest correlation is between vegetation density and browse availability

($r = 0.736$). The correlation coefficient between vegetation density and vegetation heterogeneity is similarly high at 0.699. Vegetation heterogeneity together with browse availability also have a moderate correlation coefficient of 0.559. The remaining coefficients are all below 0.5, indicating a lower degree of correlation and even weak negative correlations (Table 5).

Binary logistic regression model

Using an omnibus test, the chi-squared probability was found to be significant for its explanatory contribution compared to the null model ($p < 0.0001^{***}$). As a measure of goodness-of-fit for logistic regression models, the Nagelkerke R-squared value of 0.43 indicates a medium to strong

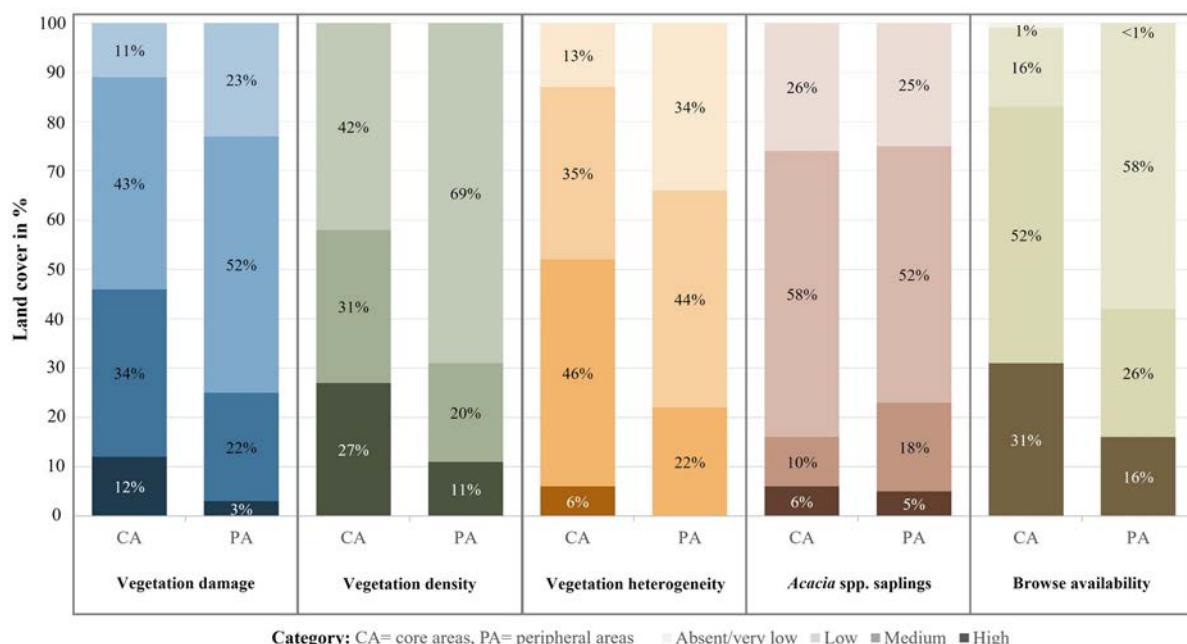


Figure 3: Effect of ecogeographical variables (EGV) (vegetation damage, vegetation density, vegetation heterogeneity, Acacia spp. saplings and browse availability) on black rhino habitat use in the Kuzikus Wildlife Reserve.

Table 4: Waterhole distribution and road use intensity by black rhino in the Kuzikus Wildlife Reserve.

Artificial habitat features		
	Core areas	Peripheral areas
Waterhole distribution		
Density	1.8/10 km ²	0.6/10 km ²
Mean distance	3.2 km	3.5 km
Road usage (frequency)		
Once a day or every second day	10.2 km	6.8 km
Every 3–4 days	37 km	15.5 km
Less than once a week	31.5 km	39.7 km

relationship and corresponds to real world phenomena (Nagelkerke 1991).

The BLRM results show vegetation heterogeneity ($p = 0.007^{**}$) and browse availability ($p = 0.008^{**}$) have the most significant effect on the utilisation of the investigated areas as rhino core range (Table 6). The number of *Acacia* spp. saplings also has a significant but negative effect ($p = 0.01^*$).

Odds ratio

Vegetation heterogeneity has the highest value ($OR = 2.2$), which means that an area is 2.2 times more likely to be used as a core area by black rhino if woody plant diversity increases. The two categories of vegetation density and browse availability would

also increase rhino occurrence by a factor of > 1.5 . The presence of waterholes and vegetation damage by rhinos have lower values ($OR = 1.3$). However, the intensity of road use and the number of *Acacia* spp. saplings have negative OR values (Table 7). Increasing the categorical values of these two variables reduces the likelihood of areas being classified as rhino core range.

DISCUSSION

Home ranges

Across the African continent, black rhino home ranges vary widely, from small (3 km^2) in humid and subtropical areas to extremely large (300 km^2) in arid areas such as northwestern Namibia (Plotz *et al.* 2016). With an average annual rainfall of approximately 210 mm, the Kuzikus Wildlife Reserve lies in the middle range of Kalahari rainfall (150–300 mm) (Wasolk & Blaum 2010). Large home range sizes would be expected in such an environment, but the maximum distribution of 115 km^2 cannot be exceeded as the perimeter fence limits the space available to rhinos. The home range sizes of rhino bulls vary considerably across the reserve, reflecting similar findings from Hluhluwe-Imfolozi Park in South Africa (Reid *et al.* 2007). At $62 \pm 28 \text{ km}^2$, the mean home range size of bulls is also smaller than in other arid rhino habitats in South Africa (Lent & Fike 2003). On the other hand, females tend to have larger territories than bulls (Reid *et al.* 2007), which is also somewhat evident here ($67 \pm 2 \text{ km}^2$).

Table 5: Matrix of correlation coefficient values between each ecogeographical variable and variance inflation factor.

	Vegetation density	Vegetation heterogeneity	Browse availability	Vegetation damage	Saplings count	Waterholes	Road use intensity
Vegetation density							
Vegetation heterogeneity	0.699						
Browse availability	0.736	0.559					
Vegetation damage	0.447	0.496	0.386				
Saplings count	0.382	0.228	0.253	0.170			
Waterholes	0.151	0.238	0.208	0.160	0.002		
Road use intensity	0.129	0.191	0.170	0.043	0.051	0.134	
Variance inflation factor	2.932	1.895	1.987	1.219	1.870	1.081	1.067

Table 6: Results of the binary logistic regression model including estimates, standard error, z and p values for each ecogeographical variable.

	Estimate	Standard error	z value	p value	Significance
(Intercept)	-4.152	0.864	-4.807	1.53e ⁰⁶	***
Vegetation density	0.612	0.340	1.799	0.072	
Vegetation heterogeneity	0.776	0.290	2.674	0.007	**
Browse availability	0.597	0.225	2.652	0.008	**
Vegetation damage	0.270	0.232	1.167	0.243	
Saplings count	-0.652	0.256	-2.549	0.011	*
Waterholes	0.286	0.682	0.419	0.675	
Road use intensity	-0.236	0.155	-1.519	0.129	

The home range and carrying capacity analysis suggests that there is insufficient space for more than two dominant rhino bulls. This should be taken into account in the population management and in the BRCP to avoid increased bull mortality due to excessive fighting. Therefore, it is recommended to remove 2–3 subadult bulls from the reserve as soon as they attain maturity and are no longer dependent on their mothers.

Seasonal shift of home ranges

In large natural environments as well as in small, fenced conditions, it is known that black rhinos and other megaherbivores shift their spatial distribution between dry and wet seasons (Shannon *et al.* 2006, Reid *et al.* 2007). The observed spatial shift of the females' home ranges towards the dune system coincided with the beginning of the *Acacia* blooming during springtime. In the Kalahari, *A. erioloba* and *A. mellifera* flower at the end of the cool, dry wintertime and set fruit before the start of the rainy season (Sekhwela & Yates 2007). In the months of September and October, all rhino cows were regularly found in this part of the reserve. During this period, *A. mellifera* flowered profusely 3–4 weeks before bushes elsewhere in the reserve. The reason the *Acacia* bloom starts earlier on the dune crest is unknown. A possible explanation might be the increased amount of sunshine due to direct exposure of the dune crests and less frost during the winter compared to the dune valleys and plains. Although rhino tolerance for more open vegetation increased during this period, isolated islands of dense bush providing cover and shade were still important as they were frequently visited and used for daytime resting.

Habitat use

The multiscale overlay of spatial habitat and vegetation information, in combination with the defined home ranges, allows us to determine how ecogeographical factors, the seasonal variation in resources, and social interactions between the individuals influence habitat use by the black rhino population in the KWR. These results correlate with the findings that herbivores typically respond adaptively to spatial and temporal changes in resource availability and suitability while significantly redesigning their environment (Owen-Smith 2010). In the Kalahari, suitable local environmental conditions are found to be a combination of high vegetation heterogeneity and high browse availability, which are the strongest predictors of rhino habitat use. This is particularly

evident around calcareous pans flanked by lunette dunes and the surrounding bushveld, which create a mosaic of microhabitats and form the core areas of all individual home ranges. These focal points regularly host the entire black rhino population at the same time, making them highly valuable congregation sites for socialising (van Rooyen *et al.* 2008).

Vegetation density, heterogeneity and browse availability

When comparing the two prominent vegetation types in the KWR, black rhino habitat use shows a clear preference for bushveld, with the three types of bushveld accounting for 70% of the core areas, compared to 71% covered by low duneveld in the peripheral areas of the home ranges. Here, the bushveld areas can be attributed to the high browse availability scores. In these areas, vegetation density is also positively correlated with browse availability. Although vegetation density was not identified as a main driving factor in habitat use, dense bush thickets or bush islands jutting out from more open landscapes were often recorded as foraging and resting sites, providing cover, shade and increased browse availability. As also shown in the arid northwest of Namibia, the intensive use of certain areas by black rhino is directly related to browse availability (Shivute 2008). In contrast, the large calcareous pans make up only about 3% of the total area and have a comparatively low browse availability value due to their sporadic or low vegetation height. Nevertheless, they are preferred and frequently visited by rhinos. This can be explained by the heterogeneity of the vegetation which is associated with a higher species composition of preferred browsable species (especially small shrubs and herbs). These foraging areas contain multiple microhabitats within a vegetation community and are selected over other areas (Buk & Knight 2010). Particularly during the dry season, this may also have a positive effect on individual fitness to compensate for the lack of nutrient intake when favourable plant species become less available (Oloo *et al.* 1994).

Damage to vegetation as a result of browsing

In the KWR, patches of vegetation with broken branches or even trees and bushes that had been completely toppled by rhinos were common. In response to browsing pressure, field observations suggest a different growth form for *Acacia erioloba*, which is more horizontal (as a result of being pushed by rhinos and continuing to grow) (Amanyanga 2017). It was also observed that isolated bushes or

Table 7: Odds ratio of each ecogeographical variable included in the binary logistic regression model.

	Vegetation density	Vegetation heterogeneity	Browse availability	Vegetation damage	Saplings count	Waterholes	Road use intensity
Odds ratio	1.844	2.173	1.816	1.310	0.521	1.331	0.790

bushes in clusters surrounded by open areas showed more damage than individuals within bush thickets. The open space around the bushes could explain why these bushes are more often targeted, as they are easier to approach and feed on. It is difficult to determine the extent to which rhinos affect plant growth in the reserve. However, there is a significant negative impact in certain areas and on certain plant species. Rhinos usually feed on a wide variety of plants, but often a limited number of species contribute to most of the ingested biomass (Loutit *et al.* 1987, Muya & Oguge 2000). This is consistent with observations of rhino feeding behaviour in the study area, while the increased feeding pressure on specific woody plant species in the KWR confirms the preference for *Acacia* species and *Grewia flava* (Shaw 2011). These are complemented by *Catophractes alexandri*, which is known to contribute a large proportion of the diet throughout Namibia, particularly in Etosha National Park (Joubert & Eloff 1971, Curtis & Mannheimer 2005). With key forage species under constant browsing pressure, with no rest for regrowth and little chance of survival, a long-term decline in browse availability can be expected. This could have negative impacts on black rhino population size and reproduction rates, as suggested by a similar scenario with *A. haematoxylon* in the southern Kalahari of South Africa (Shaw 2011). In order to adapt to the potential depletion of key resources in fenced areas through increased browsing pressure, possible measures could include reducing herbivory by fencing off severely degraded areas, managing black rhino numbers and other browsing game species that directly compete with them (Redick & Jacobs 2020). In particular, the argument for increasing the range of black rhino through land expansion should be considered.

Conversely, rhino impacts can also be positive at both macro- and microhabitat levels. Like other megaherbivores, black rhinos are considered to be ecological engineers (Owen-Smith 1998). In particular, through their feeding behaviour and dispersal, black rhinos have great potential to alter the structure of landscape vegetation. Observations in the KWR have shown that a variety of other smaller animal species benefit from the fallen branches or toppled bushes. For instance, they provide new hiding places and make leaves more accessible, increasing browse availability for springbok, common duiker and steenbok, amongst others (Amanyanga 2017). Seed pod ingestion and excretion in moist dung also aids seed dispersal and germination; germination is often higher when seeds have been previously ingested by herbivores (Miller 1995).

***Acacia* spp. saplings**

At the landscape level, the distribution of the age structure of *Acacia erioloba* in KWR is mostly

homogeneous. This means that in certain areas, young and middle-aged individuals are absent while the population continues to age. This picture clearly stands out from that of the surrounding livestock farms, where the tree population consists of a diverse age structure. The absence or limited growth of young saplings in the KWR can be attributed to the impact of browsing herbivores. On livestock farms herbivory is mostly through grazing rather than browsing; this results in higher surviving rates of saplings and in heterogeneous tree populations. Conversely, the risk of overgrowth and woody encroachment is higher on livestock farms (Riginos & Young 2007).

However, the absence of *Acacia* spp. saplings is widespread throughout the entire reserve and does not only occur in highly frequented rhino areas. A density-dependent mortality among young *Acacias* has been observed in other areas of the Kalahari, as they often do not survive in direct resource competition with similarly old individuals or with dense grass cover (Skarpe 1991, Riginos & Young 2007). Additionally, an increased mortality in middle-aged *Acacias* is also known in the region (Moustakas *et al.* 2006).

The BLRM has shown a significant negative correlation predicting habitat use of black rhinos. This means that areas which are favoured as feeding grounds have a low number of saplings. It can be assumed that these areas contained higher numbers of saplings in the past, which continuously decreased over time due to feeding pressure of the rhinos and other herbivore species and now result in the absence or low amounts of surviving individuals. It is also known that rodents as well as invertebrates can have substantial impacts on the survival rates of saplings (Riginos & Young 2007).

Artificial habitat components

No general avoidance of habitat use was observed in areas frequently traversed by vehicles. In this context, flight distances were recorded for individual rhinos, limited to an average of 200 m and varying considerably between individuals (from 0 to a maximum of 1,200 m). Here, adjacent areas of dense vegetation appear to have a positive effect on reducing flight distances compared to more open areas. In addition, it is still uncertain whether increased human activity has a direct impact on black rhino habitat use. In the KWR, contrasting scenarios were observed. First, one habituated adult bull showed minimal signs of avoiding human presence, as evidenced by its frequent proximity to residential structures. In contrast, all females and their calves appeared to actively avoid human occupied areas. However, this behaviour may also be influenced by the less favourable habitat conditions in these areas.

It is well known that black rhinos usually drink daily and often spend time at waterholes, especially at night when social gatherings are common. Waterholes therefore play an important role in the social life of rhinos (Schwabe *et al.* 2015). They also provide mud wallows, which are used for cooling down the rhinos' bodies and for skin care (Joubert & Eloff 1971). However, no direct influence of waterhole availability on rhino habitat use was found, as the waterholes are well distributed and evenly spaced across all regions of the reserve. It is possible that the likelihood of waterholes being visited regularly is affected by the surrounding suitable habitat that can be used on the way to or from the waterhole. In this context, it is worth reiterating the importance of waterholes at calcareous pans in conjunction with adjacent feeding areas, as they provide suitable areas for general daily food, minerals and water intake, as well as for social interactions, which is presumably why these habitats are used most frequently by all individuals. Artificial waterholes constructed at the pans are therefore essential to provide a constant supply of water during the dry season, while abundant rain in the wet season can flood the pans and create large lake systems.

CONCLUSION AND MANAGEMENT RECOMMENDATIONS

Given the suitable conditions and landscape characteristics for black rhino found around large calcareous pans, these findings serve as a possible explanation for the high population growth in KWR, as well as for the eastern region of Namibia (Muntifering *et al.* 2023). Successful rewilding efforts in the region have been shown to restore ecological balance and promote biodiversity, especially for threatened species such as the black rhino. With rewilding efforts, the Kalahari could become an important base for the conservation of the southwestern black rhino (*Diceros bicornis* ssp. *bicornis*) population in the future.

When considering further reintroductions of black rhino into the sparsely populated central or southern Kalahari, sites with one or more large pans in conjunction with surrounding belts of diverse and dense vegetation should be favoured. The diverse habitats and vegetation types around the pans can be used to compensate for less suitable adjacent areas. Alternatively, or in addition, riverine landscapes in this region also contain a high diversity of vegetation that could also provide suitable black rhino habitat (van Rooyen & van Rooyen 1998). By prioritising the restoration of natural processes of these characteristic landscape features, abandoned or degraded farmland containing pans and/or rivers may provide rewilding opportunities, where black rhino reintroduction can play an important role (Monbiot 2013). As natural ecosystem engineers, black rhinos are critical for

ecosystem functioning. They can shape open landscapes, reduce bush encroachment, transport seeds and nutrients, and influence species composition and carbon storage in ecosystems, which in turn may benefit other native species and the wildlife economy as a whole (Seidel *et al.* 2019).

Achieving this would require carefully considered actions (e.g., management of natural resources and reserve infrastructure, security measures, community engagement), which could help manage existing hazards, such as the high number of livestock fences or the lack of adequate water points (Emslie & Brooks 1999, Ferguson & Hanks 2010).

This information, together with the other suitability parameters of the official assessment protocol, can be used to evaluate sites for black rhino custodianship applicants in the Kalahari. In particular, the habitat objective can consider identified region-specific conditions such as the presence, size and number of pans and their surrounding vegetation heterogeneity and characteristics (MEFT 2020). This may help inform the decision-making process for assessing future rhino conservation areas to further increase the population and range of black rhino throughout the region.

RESEARCH PERMIT

For this study, an official research permit (RPIV01042024) was issued by the National Commission for Research, Science and Technology of Namibia (NCRST) with the approval of the Ministry of Environment, Forestry and Tourism in April 2021.

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